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RESEARCH ARTICLE | *Control of Movement*

The predictability of a target's motion influences gaze, head, and hand movements when trying to intercept it

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The predictability of a target's motion influences gaze, head, and hand movements when trying to intercept it. *J Neurophysiol* 121: 2416–2427, 2019. First published May 1, 2019; doi:10.1152/jn.00917.2017.—Does the predictability of a target's movement and of the interception location influence how the target is intercepted? In a first experiment, we manipulated the predictability of the interception location. A target moved along a haphazardly curved path, and subjects attempted to tap on it when it entered a hitting zone. The hitting zone was either a large ring surrounding the target's starting position (ring condition) or a small disk that became visible before the target appeared (disk condition). The interception location gradually became apparent in the ring condition, whereas it was immediately apparent in the disk condition. In the ring condition, subjects pursued the target with their gaze. Their heads and hands gradually moved in the direction of the future tap position. In the disk condition, subjects immediately directed their gaze toward the hitting zone by moving both their eyes and heads. They also moved their hands to the future tap position sooner than in the ring condition. In a second and third experiment, we made the target's movement more predictable. Although this made the targets easier to pursue, subjects now shifted their gaze to the hitting zone soon after the target appeared in the ring condition. In the disk condition, they still usually shifted their gaze to the hitting zone at the beginning of the trial. Together, the experiments show that predictability of the interception location is more important than predictability of target movement in determining how we move to intercept targets.

NEW & NOTEWORTHY We show that if people are required to intercept a target at a known location, they direct their gaze to the interception point as soon as they can rather than pursuing the target with their eyes for as long as possible. The predictability of the interception location rather than the predictability of the path to that location largely determines how the eyes, head, and hand move.

gaze; hand movements; head movements; interception

INTRODUCTION

When interacting with objects, people normally direct their gaze toward them (Johansson et al. 2001; Land and Hayhoe 2001; Mennie et al. 2007; Pelz et al. 2001; Smeets et al. 1996; for reviews, see Hayhoe and Ballard 2005; Land 2006). When objects move in the environment, people almost automatically track them with their gaze (Dorr et al. 2010; Lisberger et al. 1987), often with a combination of eye and head movements (Bahill and McDonald 1983; Brenner and Smeets 2007, 2009; Mrotek and Soechting 2007; Orban de Xivry and Lefèvre 2007; Soechting and Flanders 2008). This allows them to keep the object of interest foveated, providing the maximal spatial resolution at the target (Schütz et al. 2009). Other advantages of looking at targets when one needs to interact with them are that it helps predict the target's future trajectory (Spering et al. 2011), leading to more precise interception (Brenner and Smeets 2011; Fookien et al. 2016), and reduces the effects that irrelevant target features have on the object's apparent motion (Braun et al. 2008; de la Malla et al. 2018, 2019) leading to more accurate performance (de la Malla et al. 2017).

An important factor that has received little attention in relation to how people interact with moving targets is how the predictability of the target's movement influences action. Most of what is known about intercepting moving objects is based on studying how targets such as balls with highly predictable movement trajectories are intercepted. However, predicting how a target will continue to move is not always so straightforward. Imagine, for example, that the wind blows away some notes that you were carrying to the other side of a lawn. The notes will be moving haphazardly across the lawn, so you will probably try to track them with your gaze while gathering them. However, the notes probably cannot be tracked very smoothly, because inevitable inaccuracy in anticipating a note's future position will lead to tracking errors when this anticipated position is used to overcome the latency that is inherent in gaze control (Robinson 1965; van den Berg 1988).

If a target is moving predictably, the observer has the option of predicting where it will be some time in the future and moving their gaze to wait at that location. This would explain the anticipatory gaze shifts that are found when a target moves back and forth (Bahill and McDonald 1983; Lisberger et al.

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1981) or bounces off a hard surface (Diaz et al. 2013; Land and McLeod 2000). Anticipating where a target will be at a considerable time in the future makes it possible to successfully intercept targets even if they are not tracked accurately (Cesqui et al. 2015) or gaze is intentionally diverted from the target (López-Moliner and Brenner 2016). If a target is moving unpredictably, anticipating where it will be at a considerable time in the future is not a reliable option, unless for some reason the future location is known. Here, we systematically examine how being confronted with unpredictable target motion influences pursuit and interceptive behavior and the extent to which knowing where the target will be at some time in the future influences this.

In a first experiment, we measured gaze, head, and hand movements as subjects attempted to hit unpredictably moving targets. They were asked to hit the targets when the targets crossed into a hitting zone that was visible from the beginning of the trial. In one condition (the ring condition), the hitting zone was a large ring, so the exact position at which the target would cross the ring gradually became clearer as time progressed (Graf et al. 2005). In the other condition (the disk condition), the hitting zone was indicated by a small disk, so the exact hitting position was evident from the start. In a second experiment, the targets moved at a constant speed on straight paths to the same hitting zones, which made it easier to pursue the targets as well as always making it possible to predict where the targets had to be hit from the moment they started to move. In a last experiment, the targets moved on a limited number of (straight) trajectories to make the target's motion even more predictable.

METHODS

Subjects

Eight subjects (1 author, 1 male) took part in the first experiment (age range: 26–39 yr). Two of the subjects reported being left-handed. Five subjects (1 male, 1 left-handed) took part in both the second and third experiments (age range: 27–33 yr). Two of the subjects took part in all three experiments. Except for the author that took part in the first experiment, all subjects were naïve to the purposes of the experiments. All subjects had normal or corrected-to-normal vision. None had evident motor abnormalities. All subjects gave written, informed consent. The study was part of a program that was approved by the

ethics committee of the Faculty of Behavioral and Movement Sciences at the Vrije Universiteit Amsterdam. The experiments were carried out in accordance with the approved guidelines.

Apparatus

The three experiments were conducted in a normally illuminated room. Subjects stood in front of a large screen (Techplex 150, acrylic rear projection screen; width: 1.25 m; height: 1.00 m; tilted backward by 30° to make tapping more comfortable) onto which the stimuli were projected (In-Focus DepthQ Stereoscopic Projector; resolution 800 by 600 pixels; screen refresh rate: 120 Hz; Fig. 1A). The setup gave subjects a clear view of the stimuli as well as of their arms, hands, and fingers. Subjects were not restrained in any way and had to intercept the projected targets by tapping on them. An infrared camera (Optotrak 3020; Northern Digital) that was positioned at about shoulder height to the left of the screen measured (at 250 Hz) the position of an infrared marker attached to the nail of the index finger of the subjects' dominant hand.

Subjects were free to move in any way they wanted during the experiments. To measure their head movements, we had subjects use their teeth to hold a biteboard with a dental imprint. The positions of three infrared markers attached to the biteboard were monitored by the Optotrak. The movement of the head was inferred from the movement of the biteboard. The use of personal dental imprints means that the position of the head (and thus of the eyes) relative to the biteboard never changes, so their relative positions need to be determined only once.

Eye movements (rotations) with respect to the head were registered with a head-mounted eye-tracking system (Eyelink II; SR Research) at 500 Hz. Where subjects were looking on the screen was determined by combining the measurements of eye in head orientation from the eye tracking system with the position of the eyes and orientation of the head from the recorded biteboard marker positions.

Calibration

To relate our gaze measurements to positions of stimuli on the screen (details described in the next paragraph), we needed to know the spatial coordinates of the images on the screen. We used a pointer consisting of a rod with one tapered end and three infrared markers attached to a surface on the other end to calibrate the screen. This pointer was first calibrated by placing an additional marker at the tip of the tapered end to determine the position of the tip relative to the three markers. The rendering of images on the screen was then calibrated by placing the tip of the pointer at five consecutively

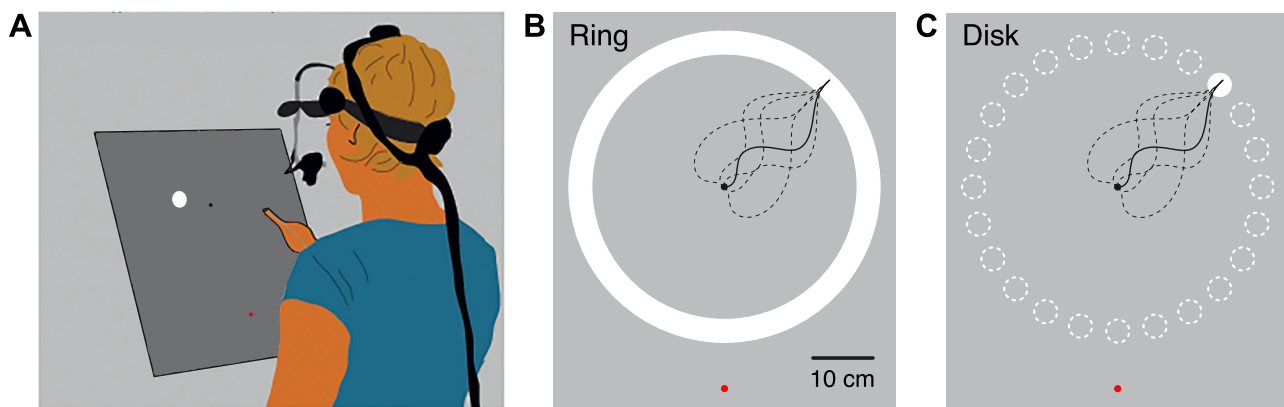


Fig. 1. Schematic representation of the task and conditions. A: subjects started with their index fingers at the red dot and had to intercept a moving target (black dot) by tapping on it when it reached the white hitting zone. B: in the ring condition, the hitting zone was always the same large white ring. C: in the disk condition, it was a small white disk at 1 of 24 possible positions. White dashed lines in C indicate the other possible positions. They were not visible during the experiment. The 6 curves in B and C show the 6 possible paths that the target could take to 1 of the 24 hitting zones.

indicated image positions on the screen. The coordinates of the image positions were determined from the positions of the three markers attached to the pointer.

The pointer and calibrated screen were used to determine the positions of the eyes relative to the biteboard. The pointer was attached to a tripod and was placed between the subject and the screen. Subjects were asked to look with one eye and move their heads until the tip of the pointer was aligned with a small white dot presented on the calibrated screen. The markers of both the biteboard and the pointer were recorded by the Optotrak. Subjects could move their heads however they wanted. Once they considered the tip of the pointer to be aligned with the current dot on the screen, they had to press the button of a mouse that they were holding in their hand. If they had moved <1 mm during the last 300 ms before doing so, a new dot appeared at a different position, and they had to repeat the procedure. Otherwise they had to press again after making sure that the alignment was still fine. Subjects had to align the tip of the pointer with 20 dots using only the left eye and then with 20 dots using only the right eye. Each time they considered the tip of the pointer and the dot to be aligned with one of their eyes, we converted the coordinates of the tip of the pointer and of the dot on the screen into a line with respect to the markers attached to the biteboard. These lines all pass through the eye, but with each measurement providing a different line with respect to the markers of the biteboard. The position with respect to the biteboard that minimized the sum of the distances to all lines was considered to be the position of the eye. From then on, we could determine the positions of the two eyes from measured positions of the markers on the biteboard.

Next, we calibrated the eye movement recordings. To do so, we presented a dot at the center of the screen and asked subjects to move their heads for 30 s while maintaining fixation on the dot. By combining the coordinates of the pupil with respect to the head from the Eyelink data with the position of the dot relative to the head (based on the calibrated screen and the biteboard marker coordinates), we determined the scaling of Eyelink coordinates that minimized the deviations in calculated gaze position throughout this period (for each eye). We verified this calibration by asking subjects to look at the screen and rendering dots at the positions at which we considered the subjects to be looking with their left and right eyes. If the two dots were at about the same place, and subjects reported that the dots were at the positions at which they were looking, the calibration was considered correct. If not, the calibration was repeated.

The final step in the calibration was to relate the position of the fingertip marker to where the subject perceived his or her finger to be relative to the projected images on the screen. For this, we measured the position of the marker on the fingertip when the subject placed the fingertip at four indicated positions on the screen. This step was performed to correct for the fact that the marker was attached to the nail rather than to the tip of the finger.

We synchronized the Optotrak recordings with the images projected on the screen by flashing a disk in the upper left corner of the screen whenever a new target appeared. A photodiode that was directed toward that part of the screen was used to briefly inactivate an additional Optotrak marker attached to the side of the screen (using custom built hardware with a delay of 1 ms). Detecting this inactivation provided information (to within the 4 ms sampling interval) about when the target appeared relative to the movement data and allowed us to determine that the average latency with which we could adjust the images to events extracted from the online Optotrak data was 24 ms. All delays were accounted for both in the analysis and in the feedback provided during the trials. Subjects did not notice that the target continued to move for ~ 24 ms before feedback about their hitting performance was provided, presumably partly because their own fingers occluded the target and partly through backward masking (Breitmeyer and Ogmen 2000).

Combining all these steps provided synchronized arm, head, and gaze information in a common coordinate system. For convenience,

we used a coordinate system that was aligned with the screen on which the target was moving so that the target and gaze could be specified by two coordinates.

Stimulus and Procedure

Experiment 1. The experiment was performed in a single session with two randomly interleaved conditions. Subjects started each trial by placing their index finger at an indicated starting point (Fig. 1A). The starting point was a 2-cm diameter red disk that was 35 cm below the screen center. One of two possible hitting zones appeared at the same time as the starting point. The hitting zone was white and 4 cm wide. It was either a ring (ring condition; Fig. 1B) or a disk (disk condition; Fig. 1C). After a random period between 0.5 and 0.7 s from when the subject placed his or her index finger on the starting position, the target appeared at the center of the screen. The target moved along a seemingly unpredictable trajectory. The target was a 2-cm diameter black disk. We chose a target that was smaller than the hitting zones, because this often elicits pursuit of the target for at least part of its trajectory when predictably moving targets are intercepted (Brenner and Smeets 2011; de la Malla et al. 2017).

Subjects had to try to intercept the target by tapping on it when it was within the hitting zone. Taps were detected online. A tap was considered to have occurred if the deceleration of the movement orthogonal to the screen was ≥ 50 m/s² whereas the finger was <5 mm above the screen. To avoid inadvertently interpreting motion onset as a tap, we also checked that the finger was moving toward the screen and that it had been lifted to ≥ 1 cm off the screen since being placed at the starting position. Whenever they wanted, subjects could rest between trials by not placing their finger at the starting position.

In the Ring condition (Fig. 1B), the white ring always appeared at the same place, centered on the screen. The ring had a radius of 25 cm and was 4 cm wide. Consequently, it extended from 23 to 27 cm from the screen center. Subjects had to hit the target when it was within the ring.

In the disk condition (Fig. 1C), the white disk appeared at one of 24 possible positions. The disk had a diameter of 4 cm (the same width as the ring), and its center was 25 cm from the screen center. The possible positions of the centers of these hitting zones were separated by 15° . Subjects had to hit the target when it was within the disk. The same target trajectories were presented in the two conditions.

The target always appeared at the center of the screen and could follow one of six possible trajectories in one of 24 directions. The different trajectories were constructed in polar coordinates using a constant increase in distance from the screen center, with the polar angle φ changing according to Eq. 1:

$$\varphi = D + \left[a + b \sin \left(2\pi \frac{t}{T} \right) \right] \left(\frac{t}{T} \right)^2, \quad (1)$$

where the D is one of the 24 directions to the hitting zone (equally spaced), t is time to reach the center of the hitting zone, and T is the movement time of the target (1.2 s). There were six combinations of values of a and b : $[-2\pi/3, \pi/2]$, $[\pi/3, -\pi/2]$, $[2\pi/3, -\pi/2]$, $[-\pi/3, \pi/2]$, $[\pi/2, \pi/2]$, $[-\pi/2, -\pi/2]$. The six possible target trajectories are shown in Fig. 1, B and C. All six trajectories crossed the centers of the hitting zones after 1.2 s. In trials of the ring condition, subjects only gradually realized where the target would pass through the large hitting zone as the trial progressed, with the target approaching the ring along a curvy path. In trials of the disk condition, subjects knew that the target was going to pass through the small hitting zone even before the target appeared.

Feedback was provided after each attempt to hit the target. A target was considered to have been hit if the tip of the finger (as calibrated) was within the outline of the target. If subjects hit the target, the target stopped moving and remained at the position at which it had been hit for 500 ms. If the tip of the finger was also within the hitting zone, a

sound indicated that the target was hit. If subjects missed the target, the target was deflected away from the finger at 1 m/s, remaining visible for 500 ms. All of the trajectories and conditions were presented in random order in a single session. In total, there were 288 trials per subject: two conditions, 24 directions to the hitting zone, and six trajectories for each direction. It took ~25 min for the experiment to be completed.

Experiment 2. The second experiment was identical to the first, except that the targets followed a straight trajectory toward either the ring or the disk (*a* and *b* in Eq. 1 were both zero). The purpose of this experiment was to determine which differences between how subjects intercepted the targets in the disk and ring conditions of *experiment 1* were due to the disk revealing where the target could be hit even before the target appeared and to determine which aspects of how subjects intercepted the targets in *experiment 1* were specific to targets that move unpredictably. In total, there were 192 trials per subject: two conditions, 24 directions to the hitting zone, and four repetitions for each hitting zone. It took ~15 min for the experiment to be completed.

Experiment 3. The third experiment was identical to the second, except that targets only moved in four of the 24 possible directions (0, 90, 180, or 270°). This made it even easier to judge where the target would cross the ring. In total, there were 40 trials per subject: two conditions, four directions to the hitting zone, and five repetitions for each hitting zone. It took ~8 min for the experiment to be completed.

Data Analysis

All analyses were performed with custom written programs using RStudio (RStudio Team 2018). In *experiment 1*, we excluded 76 trials (3.3%) in which subjects clearly did not follow the instruction. These were 52 trials in which no tap was detected, 12 trials in which the distance between where subjects tapped (the tap position) and where the target was at the moment of the tap was >20 cm, and 12 trials in which the distance between the tap position and the position at which the target's path crossed the center of the hitting zone was >20 cm. No trials were excluded due to missing data. In *experiments 2* and *3*, we excluded six (0.5%) and two (0.8%) trials, respectively, all because subjects did not tap on the screen within 1.5 s.

The next step in our analysis was to align the Optotrak and Eyelink data with the presentation of the images on the screen using the timing signal from the photodiode. Because the data acquisition itself was not synchronized with the image projection and was at different frequencies for the Optotrak and Eyelink, the first step in our analysis was to align the signals in time using linear interpolation to obtain a target position (on the screen), eye orientations (with respect to the head), eye positions (in space), head orientation (in 3 dimensions with respect to the world), and hand position (position of the finger with respect to the screen) at each moment from when the targets appeared until the moment of the tap. We refer to the average position of the two eyes as the head position, so the reported changes in head position include influences of both displacements and rotations of the head. We combined the temporally aligned positions of the eyes in space with the orientations of the eyes with respect to the head and the orientation of the head in space to calculate the line of sight for each eye.

We determined where subjects were looking on the screen (gaze) by averaging the estimates of where the lines of sight of the two eyes intersected the screen (except for 22 trials of *experiment 1* in which only 1 of the eyes was measured correctly, probably due to some light reflecting on glasses; for those trials, we used the estimates of only 1 eye). We calculated the instantaneous speed and acceleration of gaze, head, and hand movements by using finite difference approximations. We divided the change in position between 10 ms before and 10 ms after the moment in question by the 20-ms time difference between them. We calculated the gaze acceleration by dividing the difference between the gaze speeds 10 ms after and 10 ms before the moment in question by the 20-ms time difference between them. When calculat-

ing the speed of the head and the hand, we considered only the motion component parallel to the screen, because we wanted to determine the peak in the speed at which the hand moved toward the vicinity of the target. Including the motion component orthogonal to the screen would include the final tapping movement, which was often very fast so that the peak velocity would often be just before the tap. We also report the component parallel to the screen when reporting head and hand positions and distances moved.

To evaluate whether gaze, the head, and the hand were following the target, we examined how the distance from the interception point decreased during each trial. Given that the hand's starting position is below all possible target locations, the hand's initial distance differed considerably between hitting zones at the top and bottom of the screen (Fig. 1, *B* and *C*). To prevent changes in the hand's distance from the upper target locations from overshadowing those from the lower target locations when averaging across target locations, we averaged normalized distances. We obtained the latter by dividing the distance from the hand position to the tap position at each moment of time by the initial distance of the hand from the tap position. Unlike for the finger, there was no specified starting position for the head and gaze. To obtain somewhat comparable normalized distances for the head and gaze, we assumed that subjects started each trial with their heads approximately in front of the position at which the targets appeared and with their gaze directed at where the targets appeared. We divided the distances of the head and gaze from the tap position by the distance from the position at which the target appeared to where it was tapped. The latter distance was always ~25 cm, but not precisely so on each trial because the tap was not always exactly at the center of the hitting zone. With these assumptions the initial normalized distance will be one unless subjects respond before the target appears. Gaze and the head are not required to end at any particular place, so they do not have to end at zero as the hand does, although we do expect gaze to end near the tap irrespective of whether subjects pursue the target or fixate where they tap. To compare how subjects moved in the different conditions, we plotted the normalized distances of gaze, head, and hand across time for each experiment and condition. To be able to evaluate the consistency of any visible differences, the plots include the standard error across subjects at each moment.

The number of saccades per trial and whether the saccades were toward the target or toward the interception location provided additional measures of gaze behavior. Determining the number of saccades toward the target can help evaluate to what extent differences in gaze behavior result from being unable to predict how the target will move. We identified saccades using a method similar to that described in de la Malla et al. (2017). We considered the eyes to be making a saccade if the gaze speed remained above a threshold of three times the target's speed for >10 ms. Because the target did not move at a constant speed, this threshold differed slightly at different moments. Once we had detected a saccade, we determined when it ended by first localizing the maximal deceleration of gaze and then finding the moment at which gaze no longer decelerated by >5 cm/s². We used the gaze position at the end of the saccade to distinguish between saccades that contribute to keeping gaze on the target and ones that direct gaze toward the hitting zone. If a saccade ended closer to the center of the target than to the center of the disk or to the midline of the ring (both at 25 cm from the screen center), we considered it to be a saccade that served to keep gaze on the target. Otherwise, we considered it to be a saccade toward the hitting zone. We do not expect subjects to be able to pursue an unpredictably moving target very precisely, so we expect them to make more saccades when tracking the target in the ring condition in which the precise position at which one would be able to hit the target was not known in advance. We tested whether this was the case using a one-sided paired *t*-test.

We also compared hand movements in the disk and ring conditions on a number of measures using one-sided *t*-tests on subject means. We compared 1) the proportion of targets hit, 2) timing precision for hitting the target, 3) peak speed of movement of the finger, 4) time to

peak speed (how rapidly subjects responded), and 5) the directness of the movement (the distance traveled; the sum of displacements across consecutive measurements until the time of the tap). In *experiment 1*, knowing in advance where the finger's movement will need to end, as one did in the disk condition, makes it possible to plan the movement as soon as the target appears, rather than having to track the target's meandering trajectory. We predicted that this might lead to 1) more targets being hit, 2) timing being more precise, 3) the mean peak speed being higher, 4) the mean peak speed occurring earlier, and 5) the movements being more direct in the disk condition. Because the subjects were the same in both conditions, we used paired *t*-tests.

In *experiments 2* and *3*, the position at which the finger's movement will end is still known earlier in the disk condition, but the straight trajectories allow one to infer where the target is to be hit as soon as it starts moving (i.e., immediately after it appears) in the ring condition. Thus, although the direction of any differences between the conditions would be expected to be the same as for *experiment 1*, we expect all the differences between conditions to be smaller. We expect the behavior of the finger in both conditions to be similar to that in the disk condition of *experiment 1*. The peak speed might still occur slightly later in the ring condition because the interception point is revealed only by the target's motion, rather than being revealed even before the target appears (by the position of the disk). Because the target trajectories were simpler in *experiment 2* than in *experiment 1* and were even more predictable in *experiment 3*, we expected performance to become better in consecutive experiments (more targets hit and better timing) and the movements to possibly also become faster and occur earlier. We used one-sided paired tests when comparing *experiments 2* and *3*, but tests were not paired when those experiments were compared with *experiment 1* because the subjects were not all the same.

RESULTS

Experiment 1: Unpredictable Trajectories

The subjects' goal was to tap on the screen in such a manner that their fingertips were within both the target and the hitting zone at the time of the tap. Subjects successfully hit more targets in the disk condition than in the ring condition (Table 1). On average, subjects tapped at the correct place (25 cm from the screen center) and time (1.2 s after the target appeared) in both conditions, but the variability (standard deviation) in the time at which individual subjects tapped was smaller in the disk condition than in the ring condition (Table 2). Thus, their timing was more precise in the disk condition.

Figure 2 shows two example trials from a representative subject for *experiment 1*. There are clear differences between how the subject moved to intercept the targets in the two conditions. When the position at which to hit the target was not

Table 2. Variability in the timing of the hits

Experiment	Disk	Ring	One-Sided Paired <i>t</i> -Tests
1	36	48	$t_7 = 2.72, P = 0.015$
2	33	44	$t_4 = 1.48, P = 0.11$
3	26	28	$t_4 = 0.71, P = 0.26$

Values are SD in ms. Performance differed significantly only between the disk and ring condition in *experiment 1*. Performance in *experiment 3* differed significantly from that in *experiment 1* (disk: $t_{7,4} = 1.92, P = 0.04$; ring: $t_{7,4} = 3.05, P = 0.008$), but the other differences between experiments were not significant.

known in advance (ring condition; Fig. 2, *left*), the gaze (blue) more or less followed the target's movement (gray) until the moment of the tap. It did so in quite a jerky manner, presumably because the eyes made many saccades to correct for errors in predicting how the target would proceed. Therefore, these saccades are not really to catch up with the target position but anticipating where the target will be next and thus often anticipating incorrect positions because the target moves unpredictably. When the position at which to hit the target was known in advance (disk condition; Fig. 2, *right*), gaze was immediately directed toward this position; the blue curve starts and remains close to the disk rather than following the target. Both the head and the hand also moved sooner in the direction of the hitting zone in the disk condition than in the ring condition; a smaller part of the trajectory is clearly red or green. One can also see that the hand moves along a straighter path in the disk than in the ring condition.

The differences between the two example trials of Fig. 2 are characteristic of the differences between the two conditions for this subject (Fig. 3) as well as for other subjects. Due to the time period between the subject placing his or her finger at the starting position and the target appearing, gaze was usually no longer directed at the starting position by the time the target appeared. In the ring condition, gaze was usually directed at the center of the screen, where the targets appeared, and then tracked the target. In the disk condition, gaze was often already directed toward the hitting zone by the time the target appeared, as is the case in the trial shown in Fig. 2 (the hitting zone was visible well before the target appeared). On some other trials of this condition, gaze was directed at the center of the screen until the target appeared, but when the target appeared a saccade was made to the disk rather than gaze tracking the target.

To illustrate the time course of the gaze movements, we plotted the average normalized distance of gaze from the tap position as a function of the time to hit the target (Fig. 4A). There is a clear difference between the ring and the disk condition. In the ring condition, the distance between the gaze and the tap position decreases constantly across time at a similar pace as the target approaches the tap position (thin black dotted line). This is consistent with subjects trying to track the target with their eyes. As could be expected on the basis of Figs. 2 and 3, on average subjects were already looking closer to the hitting zone when the target appeared in the disk condition (dashed blue curve lower than solid blue curve from the start in Fig. 4A). Consequently, the distance between gaze and the tap position changed much less across time. The average normalized distance between gaze and tap position decreased to only ~ 0.2 in both conditions (Fig. 4A). This corresponds to a distance of ~ 5 cm at the moment of the tap.

Table 1. Percentage of targets hit

Experiment	Disk	Ring	One-Sided Paired <i>t</i> -Tests
1	72.2	57.4	$t_7 = 3.36, P = 0.006$
2	83.8	85.4	$t_4 = 2.02, P = 0.94$
3	86.0	94.0	$t_4 = 1.73, P = 0.92$

A target is considered to have been hit if the finger, as calibrated, was within the bounds of both the target and the hitting zone at the time of the tap. Performance differed significantly only between the disk and ring condition in *experiment 1*. Performance in *experiments 2* and *3* differed significantly from that in *experiment 1* (*experiment 2*, disk: $t_{4,7} = 2.3, P = 0.03$; ring: $t_{4,7} = 5.12, P = 0.0003$; *experiment 3*, disk: $t_{4,7} = 2.34, P = 0.03$; ring: $t_{4,7} = 7.02, P < 0.001$) but not from each other (disk: $t_{4,4} = 0.33, P = 0.38$; ring: $t_{4,4} = 1.46, P = 0.09$).

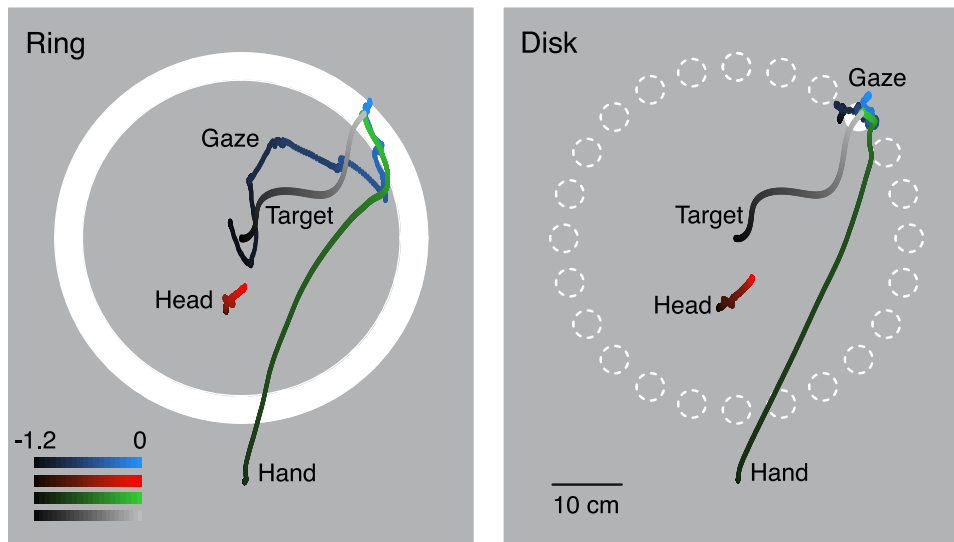


Fig. 2. Example of gaze, head, and hand movements on single trials for a representative subject in the 2 conditions of *experiment 1*. Data of 2 trials with the same target trajectory from the moment the target appeared until the time of the tap. The colors of the curves change with the remaining time to tap: from black to either gray, blue, red, or green (for the target, gaze, head, and hand, respectively).

This could mean that gaze was not directed at the position that was tapped, but it could also arise from measurement errors (see DISCUSSION). We never required subjects to fixate a specific position during the experiment, to avoid biasing where they looked, so we did not try to correct for systematic shifts (such as the overall shift to the upper right in Fig. 3, *left*), for instance, by assuming that on average subjects were looking at the disks when they hit the targets, because we cannot be sure that this was the case. Importantly, the differences that we find between the two conditions cannot be due to eye-tracker shifts because the trials of the two conditions were interleaved.

A closer look at the tracking strategy (Fig. 4A, *inset*) reveals that subjects made more than twice as many saccades in the ring than in the disk condition ($t_7 = 8.9$, $P < 0.001$). In accordance with subjects trying to keep their eyes on the unpredictably moving target in the ring condition, we see that the increase in the number of saccades is caused by an increase in the number of saccades directed to the target ($t_7 = 11.4$, $P < 0.001$).

The movements of the head and the hand also differed between the two conditions (Fig. 4, *B* and *C*). The head was closer to the hitting zone in the disk condition than in the ring condition from the moment the target appeared (dashed red curve lower than solid red curve). At least part of this difference in head position is probably related to the above-mentioned difference in gaze; one can orient one's head toward the position at which the target is to be hit before the target appears in the disk condition but not in the ring condition. The hand was not allowed to start moving before the target appeared, so it always started at a normalized distance of 1. It took some time for the hand to start moving when the target appeared. Once the hand did start moving, it approached the tap position sooner in the disk condition than in the ring condition.

In accordance with the impression one gets from the gaze panels of Figs. 2, 3, and 4A, the distance traveled by gaze while the target was present was longer in the ring condition than in the disk condition (53 ± 4 vs. 32 ± 3 cm, means \pm SE across subjects; $t_7 = 6.3$, $P = 0.0002$). This is consistent with subjects trying to pursue the target in the ring condition but not in the disk condition.

Unlike gaze, the head does not travel significantly less in the disk condition ($t_7 = 1.11$, $P = 0.15$); it travels an average of 8.2 ± 0.9 cm. The peak speed of the head was not significantly higher ($t_7 = -6.2$, $P = 0.99$) in the disk (18 ± 2 cm/s) than in the ring condition (21 ± 2 cm/s). However, the head did reach the peak speed earlier in the disk condition ($t_7 = 4.86$, $P = 0.0009$); the peak speed occurred after 0.71 ± 0.05 s in the disk condition and after 0.89 ± 0.03 s in the ring condition. The hand trajectories were straighter (shorter) in the disk condition ($t_7 = 6.20$, $P = 0.0002$); the mean distance traveled by the hand was 43.4 ± 0.3 cm in the disk condition and 51.6 ± 1.4 cm in the ring condition. Despite the shorter distance, the peak speed of the hand was higher in the disk condition; it was 122 ± 3 cm/s in the disk condition and 112 ± 5 cm/s in the ring condition ($t_7 = 2.5$, $P = 0.02$). The peak speed of the hand also occurred earlier ($t_7 = 3.44$, $P = 0.005$) in the disk condition (0.52 ± 0.03 s) than in the ring condition (0.65 ± 0.05 s). These findings support the idea that knowing in advance where they will hit the target allows subjects to move sooner, more directly, and faster.

The location at which subjects will be able to hit the target only gradually became apparent in the ring condition. When the ring appeared and the target started to move, subjects could have followed the strategy of moving their hand directly to some position within the ring and adjust their movement along the ring as the target approached it. Figure 5 shows that they did not do this. They seldom moved along the ring (Fig. 5, *left*). Furthermore, when the target was to be hit at the closest position to the hand's starting position, subjects moved their hands toward the target, within the ring, before moving them back down to the ring as the target approached the ring (Fig. 5, *bottom left*). In the disk condition (Fig. 5, *right*), subjects moved their hands to the hitting zone along a much straighter path, moving beyond the hitting zone only when the hitting zone was near the hand's starting position (Fig. 5, *bottom right*) a single time.

Experiment 2: Predictable Trajectories

The first experiment showed a marked difference in movement strategies between the two conditions. We attribute the difference to the predictability of the interception location. In

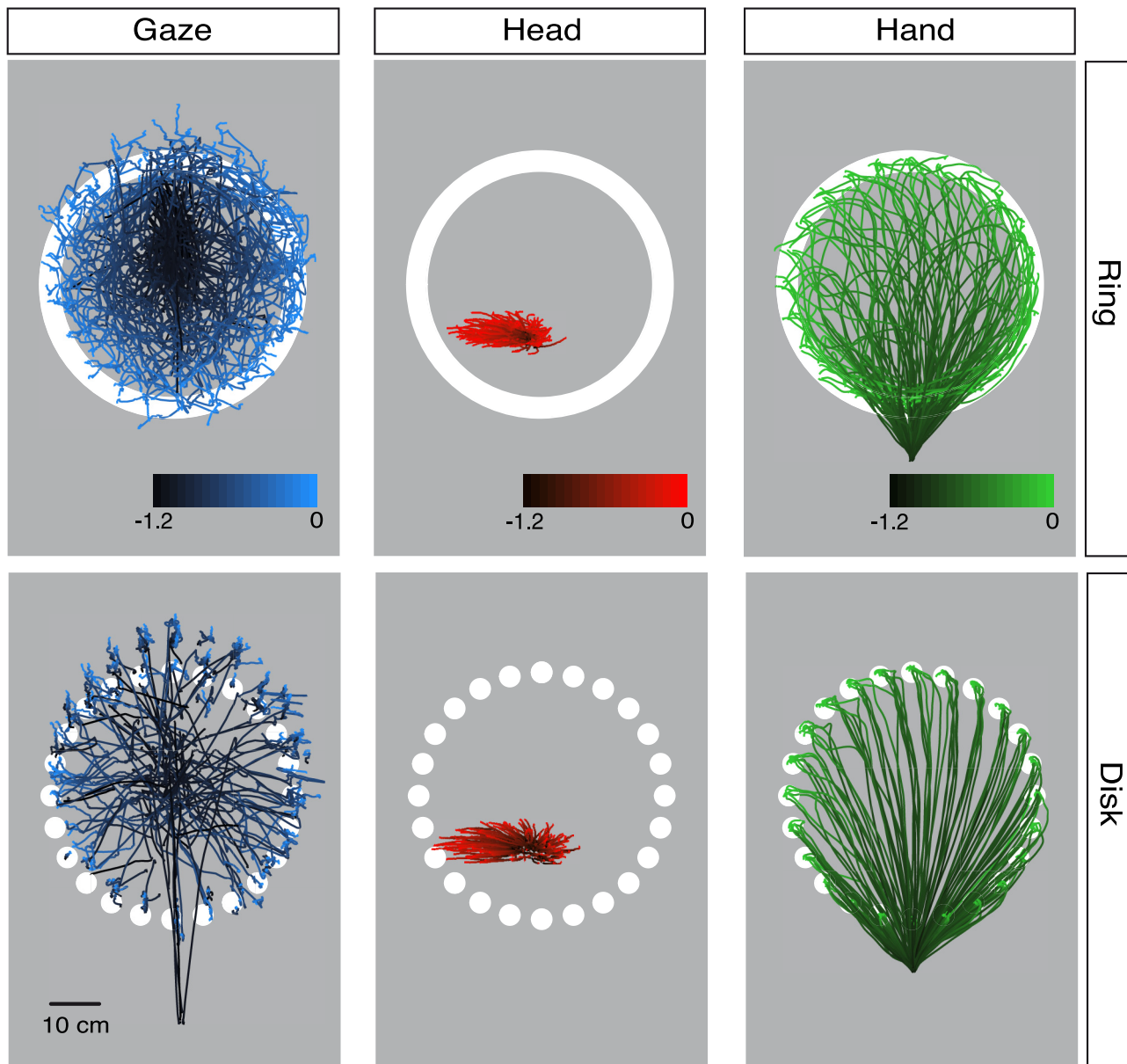


Fig. 3. Gaze, head, and hand movements of all trials of the same representative subject in *experiment 1* shown in Fig. 2. Colors change from black to blue (gaze), red (head), and green (hand) across time from when the target appears to the moment of the tap (as in Fig. 2).

the second experiment, we kept the conditions the same, but the interception location was predictable from just after the targets appearing and started moving because the targets moved at a constant velocity along straight paths. Subjects managed to hit more targets when the targets moved more predictably, and there was no longer a significant difference between the disk and ring conditions (Table 1). The variability in the timing of the taps was also no longer significantly larger in the ring than in the disk condition (Table 2). Therefore, the differences in performance between the two conditions were not due just to the interception location being known before the target appeared in the disk condition.

The tap accuracy and timing were similar in the ring and disk conditions (Table 1 and 2), but there were small differences between the two conditions. On average, gaze traveled less in the disk (33.2 ± 3 cm) than in the ring (48.6 ± 3 cm) condition. The difference was not consistent across subjects

($t_4 = 1.7$, $P = 0.08$) and is easily explained by the interception location being known before the target appears in the disk condition, whereas it only becomes apparent from the motion of the target in the ring condition (it is evident as soon as the target moves because the target always moves along a straight path). Gaze was often already at the interception location by the time the target appeared in the disk condition, whereas it could move there only after the target started moving in the ring condition (Fig. 4D). That the time at which the interception location is known is important is also evident from the difference between gaze in the ring conditions of *experiments 1* and 2; gaze reaches the vicinity of the tap position earlier in *experiment 2* (compare Fig. 4, A and D). In *experiment 1*, it took an average of 1.04 s for gaze to be within 10% of the final normalized distance to the tap position. In *experiment 2* it only took 0.79 s ($t_{4,7} = 3.84$, $P = 0.003$). This difference is undoubtedly the result of the predictable target motion revealing

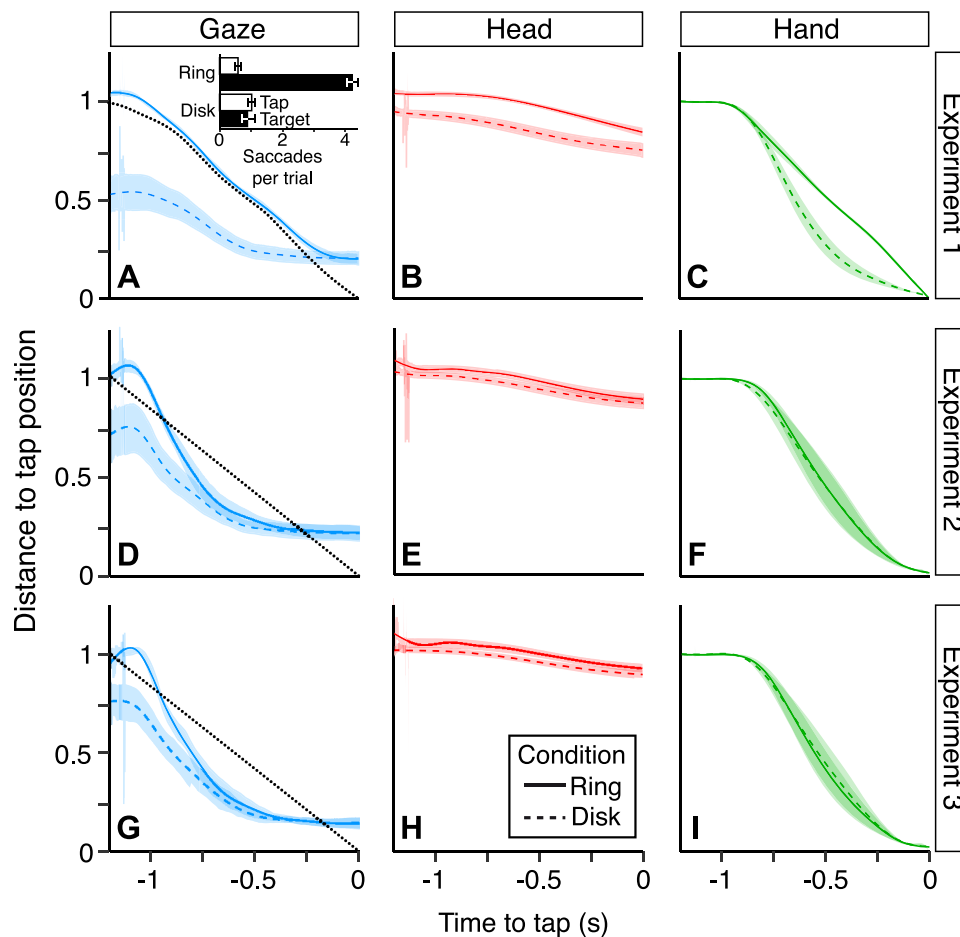


Fig. 4. Analysis of the average gaze, head, and hand movements of all 8 subjects in *experiment 1* (A–C) and all 5 subjects in *experiments 2* (D–F) and *3* (G–I). Normalized distance to the tap position as a function of the time until the target is hit for the gaze, head, and hand. Lines (continuous for the ring condition, dashed for the disk condition) and shaded areas are the means and SE of the subjects' individual mean values. A normalized distance of 0 corresponds to being at the tap position. A normalized distance of 1 corresponds to being where the target appeared for the gaze and the head and corresponds to being at the finger's starting position for the hand. In the gaze graphs, we also show the mean normalized distance of the target from the tap position (black dotted curve). A, inset, shows the number of saccades per trial in *experiment 1*, which were split by whether saccades ended closer to the target (black bars) or closer to the tap position (open bars). Error bars are SE across the subjects' mean number of saccades.

the interception location. However, the difference in performance between the disk conditions of *experiments 1* and *2* (Table 1) suggests that there is also a direct effect of the predictability of target motion.

The difference in head position between the two conditions is smaller in *experiment 2* (Fig. 4E) than in *experiment 1* (Fig. 4B) from the moment that the target appears, although there is no difference between the experiments in terms of the available information at that moment. The difference is consistent with the difference in gaze at the moment the target appears also being smaller in *experiment 2* than in *experiment 1*. Thus, the differences in head movement between the conditions are probably due to differences in gaze. The differences in gaze between the two experiments might be the result of the initial target trajectory always being informative in *experiment 2*.

The hand movements were extremely similar in the disk and ring conditions of *experiment 2* (Fig. 4F), with the hand traveling 42.1 cm in both cases. The small difference in movement onset is consistent with the hitting position becoming apparent slightly later for the ring than for the disk condition. The hand did not appear to move as quickly to the hitting zone in this experiment as it had in the disk condition of *experiment 1*. The peak speed was 110 ± 8 cm/s for the disk condition and 107 ± 7 cm/s for the ring condition ($t_4 = 1.92$, $P = 0.06$), which are values close to the peak velocity of the hand for the ring condition in *experiment 1* (113 cm/s). The peak speed occurred after 0.6 s for both conditions, which is midway

between the values that we found for the disk and ring conditions in *experiment 1*. The results of this experiment support the idea that knowing that the target's initial movement will be informative of the interception location on all trials influences how subjects approach the task.

Experiment 3: Predictable Trajectories and Tap Positions

In *experiment 2* we found that the predictability of the hitting position influences interceptive actions. In *experiment 3*, we investigated whether the degree of predictability was important. To do so, we made it even easier to predict where the targets will be hit in the ring condition. We repeated the second experiment, but with only four of the 24 hitting zones (values of D in Eq. 1 of 0, 90, 180, and 270°). The percentage of targets that were hit was highest in this experiment, albeit not significantly higher than in *experiment 2* (Table 1). The percentage of targets that were hit was not lower for the ring condition (94%) than for the disk condition (86%). The standard deviation in timing the hits was lowest in this experiment, albeit not significantly lower than in *experiment 2* (Table 2).

The time course of the movements in *experiment 3* was very similar to that in *experiment 2* (Fig. 4, G–I). Again, the main difference between the ring and disk conditions is that gaze was directed to the hitting zone before the target appeared in the disk condition, whereas it obviously could not be in the ring condition. Movements of the head hardly contributed to this

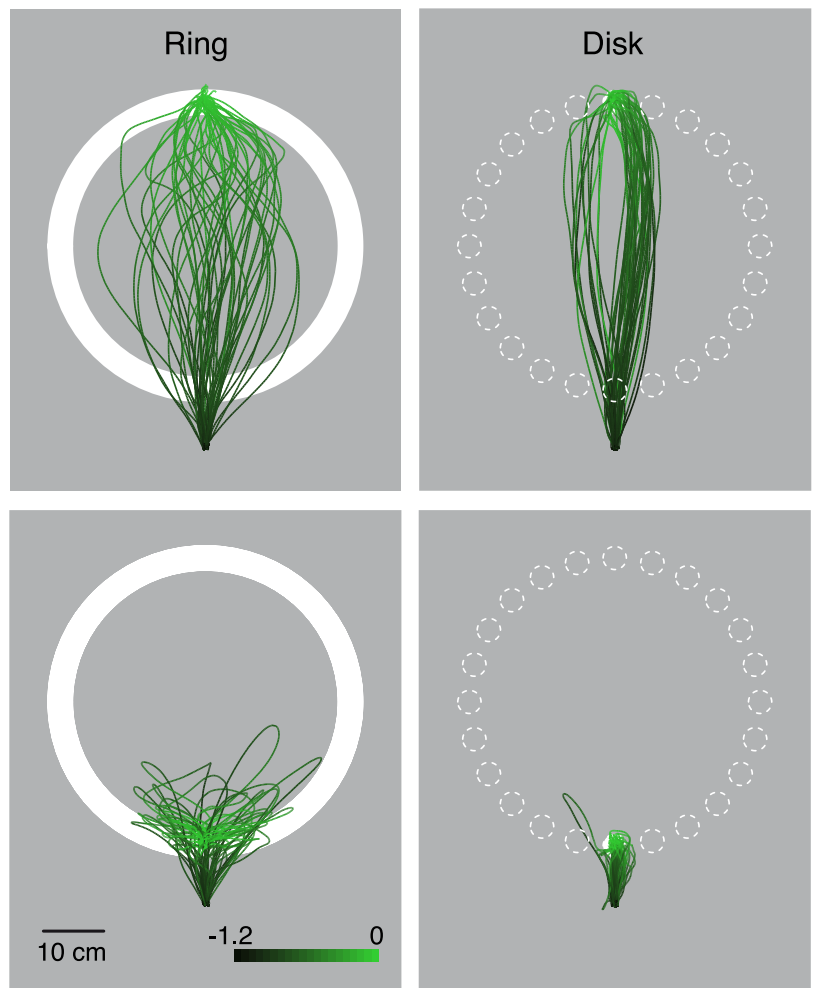


Fig. 5. Hand movements of all trials of all 8 subjects for the furthest (*top*) and the nearest (*bottom*) hitting zones in *experiment 1*. All trajectories start at the hand's starting point near the bottom of the panel. Color changes from black to green across time, as in Figs. 2 and 3.

difference, and the arm movements were not affected by knowing where the target would be hit in advance. Even the tiny delay in hand movement onset seems to have vanished, probably because it is easier to tell in which of the four directions the target is moving than to distinguish between 24 directions. The peak speed of the hand (102 ± 6 cm/s) and the time at which it occurred (0.59 s after appearing, when the target was almost halfway to the interception location) were similar to the values in *experiment 2* ($t_{4,4} = 1.51$, $P = 0.90$, and $t_{4,4} = -0.06$, $P = 0.52$, for the peak speed and the time at which it occurred, respectively). The fact that again performance was slightly different from that of the disk condition of *experiment 1* supports the notion that besides the target's path being relevant because it influences when one knows where the target is to be hit, it is presumably also easier to determine when the target will arrive at the position at which it is to be hit when the target is moving more predictably.

DISCUSSION

What options does one have to successfully intercept a target that moves unpredictably? When one tries to catch a note that is blown away by the wind, the only option is to track it with one's gaze as one adjusts one's arm movement so that the hand reaches the note. When trying to intercept a predictably moving object, one could follow the same

strategy, but one could also predict where one will be able to intercept the target and immediately direct one's gaze and movement toward that location. We examined how the circumstances influence what people do and how the choice influences their performance.

The results of *experiment 1* suggest that even if the target moves in an unpredictable manner, so that it is essential to constantly monitor its motion, pursuing the target with one's gaze is not always the best strategy for guiding the hit. To pursue a target smoothly with no delay, one must be able to anticipate how it will continue moving (Lisberger et al. 1981; Kowler and Steinman 1979). If a target's trajectory is completely unpredictable (ring condition of *experiment 1*), gaze must track the target (Figs. 2, 3, and 4A), even if this means that pursuit of the target will be interspersed with saccades (Fig. 4A, inset). Such saccades will temporarily limit what one perceives (Bridgeman et al. 1975; Burr et al. 1999; Castet and Masson 2000; Majj et al. 2012; Ross et al. 2001; Zuber and Stark 1966) and give rise to errors in judging the target's position and motion (Goettker et al. 2018, 2019; Honda 1989; Mateeff 1978; Matin and Pearce 1965; Majj et al. 2009, 2011; Matziridi et al. 2015; Morrone et al. 1997; Schlag and Schlag-Rey 2002). If one knows where one will be able to hit the target in advance (imagine waiting for a fly to settle on a particular breadcrumb that it is clearly circling around; disk condition), it appears to be better to quickly direct one's gaze toward that

position and track its approach with peripheral vision (Fig. 4A), because doing so appears to improve performance (Tables 1 and 2). That performance is better when fixating in such circumstances need not be due to the disadvantages associated with having to perform saccades to keep the target in central vision outweighing the disadvantages of relying on peripheral vision to track the target's motion, because being able to anticipate where one will be able to hit the target may be advantageous for other reasons. However, the fact that subjects did not consistently pursue the target in the disk condition trials, although they did pursue the target on the interleaved ring condition trials, suggests that fixating is advantageous under these circumstances.

As mentioned in the results, it seems surprising that subjects appeared not to direct their gaze exactly at the tap position at the moment of the tap (Fig. 4, A, D, and 4G). To not bias their gaze behavior, we did not give them instructions about where to look at any time, except during the eye movement calibration, during which subjects fixated a static dot (see METHODS). The measured precision during calibration was $\sim 0.7^\circ$ horizontally and 1.2° vertically for each eye (root mean square deviation). However, recorded eye orientations are known to drift, due mainly to headband slippage, giving rise to systematic shifts. Therefore, we cannot determine with certainty which part of the distance between gaze and tap position at the moment of the tap is due to measurement errors and which is due to the fact that subjects may not have directed their gaze precisely at the tap position when tapping.

Our results are largely in agreement with previous studies on how people interact with unpredictable moving targets (Danion and Flanagan 2018; Mrotek and Soechting 2007; Xia and Barnes 1999). Danion and Flanagan (2018) examined subjects' gaze strategy when tracking a target that moved along an unpredictable trajectory. In one condition their subjects had to track a target with their hand without instructions about gaze. They found that gaze also always tracked the target. This is consistent with our observation that subjects track unpredictable target motion if they do not know how the target will move. Mrotek and Soechting (2007) examined subjects' gaze strategy in an interception task. In their task, subjects were free to choose when and where to hit the targets. They observed that subjects pursued the target but also that saccades were suppressed just before the moment of interception. This is consistent with our proposal that making saccades near the time of interception comes at a cost. However, the cost cannot be very high because people do in some circumstances make saccades to where they are required to hit a target before reaching it with the hand (rather than pursuing it smoothly until it is hit) when the target moves predictably (de la Malla et al. 2017).

In both the disk and ring conditions, the target has to be hit at a specific time and place. This restricts the adjustments that subjects can make when guiding the hand to the target (Brenner and Smeets 2015). When the target's trajectory is unpredictable, knowing where to hit it in advance might not improve the timing of the tap (*experiment 1*; Table 2) through its influence on the eye movements but by making it easier to judge when to hit the target. The targets moved quite smoothly, so knowing that they will pass a certain position probably helped estimate when that would happen. However, judging when the target will cross the ring is less

reliable because a small change in the trajectory that is constantly curving can change the position at which the target crosses the ring and, therefore, also the time at which it does so at its current speed. The hand must also reach the changed position. The hand followed the target to some extent in the ring condition of *experiment 1*. Subjects did not quickly move their hands to the ring and then adjust their position along the ring (Fig. 5), but the hands did not closely track the target either (Fig. 2). This may just be due to physical limitations in how the hand can be moved, but subjects may intentionally avoid occluding the target with the hand, or even avoid occluding parts of the screen across which the target may move during its meanderings.

The predictability of the targets' trajectories also influenced head movements to some extent. Previous studies have reported that head movements contribute substantially to keeping moving targets in central vision when interacting with them (Bahill and LaRitz 1984; Fogt and Persson 2017; Fogt and Zimmerman 2014; Mann et al. 2013). Most of those studies involved sports such as baseball or cricket, in which the ball's angular displacement near the time of the hit is so large that it is impossible to track the ball by moving the eyes only. In our study, the distance between where the targets appeared and the hitting zone was only 25 cm ($\sim 25^\circ$, depending on where the subject chose to stand), so large head movements were not necessary to keep track of the moving targets. However, head movements did contribute to the changes in gaze (Fig. 4, B, E, and H). The contribution was modest, but the differences between the conditions were more or less consistent with the differences in gaze, although gaze changed more and more abruptly.

In summary, for the conditions used in the current study, the preferred strategy was to quickly direct one's gaze at the position at which the target will be hit. Gaze only tracked the target when the interception point was initially unknown (ring condition) and could not immediately be inferred from the target's motion (*experiment 1*). In that case, performance was relatively poor, presumably because it was impossible to keep one's eyes on the target and because the hand movement was constantly adjusted as a result of it being difficult to anticipate when and where the target could be hit. The experiments suggest that how people approach an interception task is determined mainly by how reliably they can predict the interception location rather than by how reliably they can predict the target's movement to that location, at least when an interception zone is specified.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

C.d.I.M., S.K.R., and E.B. conceived and designed research; C.d.I.M. performed experiments; C.d.I.M. analyzed data; C.d.I.M., S.K.R., J.B.J.S., and E.B. interpreted results of experiments; C.d.I.M. prepared figures; C.d.I.M., J.B.J.S., and E.B. drafted manuscript; C.d.I.M., S.K.R., K.C., J.B.J.S., and E.B.

edited and revised manuscript; C.d.l.M., S.K.R., K.C., J.B.J.S., and E.B. approved final version of manuscript.

ENDNOTE

At the request of the authors, readers are herein alerted to the fact that data supporting these findings are available through the Open Science Framework at <https://osf.io/dfkbg/>. These materials are not a part of this article and have not undergone peer review by the American Physiological Society (APS). APS and the journal editors take no responsibility for these materials, for the website address, or for any links to or from it.

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